

## Defoliation of trees in roadside corridors and remnant vegetation in the Western Australian wheatbelt

J J van Schagen<sup>1</sup>, R J Hobbs<sup>2</sup> & J D Majer<sup>3</sup>

<sup>1</sup>Agriculture Protection Board, Baron-Hay Court, South Perth WA 6151

<sup>2</sup>CSIRO Division of Wildlife and Ecology, LMB No 4 PO, Midland WA 6056

<sup>3</sup>School of Biology, Curtin University of Technology, GPO Box U 1987, Perth WA 6001

Manuscript received December 1991; accepted April 1992

### Abstract

We compared the abundance and impact of caterpillars of the bag-shelter moth (*Ochrogaster lunifer*) on trees of *Acacia acuminata* on road verges and within a large reserve in the Western Australian wheatbelt. Caterpillars were observed to cause severe damage to roadside trees during an outbreak of the insect in 1987 and 1988. The caterpillars live communally in a bag which develops on a tree branch. Within the reserve, bags were present early in the season but failed to develop and no caterpillars reached maturity. On road verges, the number of bags per tree was significantly greater on narrow verges than on medium or wide verges. An individual colony consumed foliage estimated to be equivalent to that carried by a tree 2 m tall. Colonies were found only on trees greater than 2 m tall, and abundance increased with tree size. Caterpillars significantly affected the numbers of leaves present on tagged shoots on trees in road verges, and defoliated shoots produced a flush of new leaves. Foliar N and P were significantly higher in mature leaves on road verges than in the reserve, and soil N was also higher on road verges. We suggest that ecological processes are significantly modified in road verges, especially narrow verges, compared with intact vegetation, and that this has important implications for corridor management. Intensive management of narrow corridors, or widening of these corridors, is required for their long-term persistence.

### Introduction

Despite recent debate about the relative merits of corridors (or linear fragments connecting larger remnants) for nature conservation (Simberloff & Cox 1987, Noss 1987), it is generally considered that vegetation corridors can have many landscape values, both aesthetically and economically, and that they may act as wildlife habitat and as conduits for faunal movement (Harris & Scheck 1991, Loney & Hobbs 1991, Saunders & Hobbs 1991). Because of their importance in the landscape, it is important that we develop an understanding of corridor ecology and dynamics.

Fragmentation of natural landscapes results in the replacement of a continuous cover of native vegetation with a patchwork of vegetation remnants embedded in a matrix which is substantially modified by agriculture or other land uses. The fragmentation process leads to many physical and biological changes, with biota in remnant patches being subjected to altered microclimatic, nutrient and hydrologic regimes, reduction in available habitat and isolation from surrounding areas (Saunders *et al.* 1991). Corridors are particularly likely to be affected by the physical and biological effects of fragmentation due to their high edge:area ratio and their juxtaposition with human transport routes and utilities (Loney & Hobbs 1991). Narrow corridors are particularly open to the influence of the surrounding matrix and can be susceptible to weed invasion, nutrient increase and increased predation risk (Panetta & Hopkins 1991, Cale & Hobbs 1991, Soul & Gilpin 1991).

In this paper, we investigate the possibility that ecological processes are liable to be markedly different between corridor vegetation and vegetation in larger remnant areas. We present a study of herbivory by the bag-shelter moth

(*Ochrogaster lunifer* Herrich-Schaeffer; Lepidoptera, Thaumetopoeidae) on populations of the tree *Acacia acuminata* Benth. on road verges and within a large nature reserve in the Western Australian wheatbelt. This area has been extensively cleared for agriculture over the past century, leaving native vegetation only in relatively small remnant areas and along roadsides (Saunders 1989). Less than 10% of the original native vegetation remains (Beard & Sprenger 1984) and woodland types are poorly represented in conservation reserves. Roadside populations of trees such as *A. acuminata* thus represent an important component of the remaining woodland vegetation. *O. lunifer* is an important defoliator of *A. acuminata* in the Western Australian wheatbelt (Mills 1951, 1952), and of other tree species elsewhere in Australia (Turner 1921, McFarland 1979). It is univoltine, with 6 larval instars occurring from January to June, and adults in November and December. Larvae are gregarious feeders and live together in a bag made of frass and cast skins covered with silk (Van Schagen *et al.* 1992). At the time our study commenced (in 1987), *O. lunifer* was in outbreak, causing severe damage to *A. acuminata* trees on road verges. Caterpillars appear to move freely within individual trees and can also move between trees.

We studied the incidence and impact of *O. lunifer* caterpillars over two years. We assessed the numbers of insect colonies and estimated herbivory levels along road verges and within the nature reserve. We also examined the possible impact of soil and foliar nutrient levels on herbivory. We aimed to assess the differences in herbivore damage between intact vegetation within the reserve and the more disturbed vegetation along roadside corridors.

### Methods

This study was conducted in a 20 x 20 km area centred on Durokoppin Nature Reserve (117° 45' E, 31° 24' S), north of Kellerberrin, about 200 km E of Perth, Western Australia.

lia. Kellerberrin has a mediterranean-type climate, with cool wet winters and hot, dry summers and an average annual rainfall of around 340 mm. The wheatbelt region is mainly agricultural land, with numerous small patches of native vegetation interconnected to varying degrees by 'corridors' of native vegetation. Recent estimates indicate that remnant vegetation comprises only 5.7 percent of the 20 x 20 km study area (Saunders *et al.* 1987). Durokoppin Reserve is the largest remnant in the area (1030 ha) and comprises a mixture of woodland, heath and shrubland (Hobbs *et al.* 1989).

A range of sites was selected within the study area. These included stands of *A. acuminata* within Durokoppin Nature Reserve, wide stands of *A. acuminata* along main or minor roads (>20 m wide), verges of medium width along major roads (≈10 m wide) and narrow road verges (<5 m wide) along gravel roads that form a network through the agricultural areas. These minor road verges often contained single rows of *A. acuminata*. Within Durokoppin reserve, *A. acuminata* occurs in open woodland with *Eucalyptus loxophleba* Benth., mostly in isolated patches of 5-10 ha. *A. acuminata* woodland comprises about 4% of the total area of the reserve (Hobbs *et al.* 1989).

In April 1987 and 1988, the conspicuous bag-shelters, which contain the caterpillars of *O. lunifer*, were counted along 100 m transects at 1 km intervals along all of the three types of road verge which occurred in the study area.

Six sites were selected within the study area in early 1987, in order to compare populations of *O. lunifer* in road verges with those in the nature reserve, and also to determine the relationship between tree size and the number of bag-shelters per tree. Three sites were within Durokoppin Nature Reserve and three were on narrow road verges. The trees were divided into five size categories, namely 0-1.9 m, 2-3.9 m, 4-5.9 m, 6-7.9 m and >8 m height, although the latter two categories were absent from the reserve. Six trees of each category were randomly chosen in each of the six areas and the number of bag-shelters per tree was counted.

To determine the amount of foliage consumed by the caterpillars, enclosures made of 1 mm nylon mesh (each 80 x 50 cm) were placed around branches of *A. acuminata* at two sites, one within a dense stand of *A. acuminata* in the reserve, the other along a narrow road verge. Eight trees in each site were selected at random shortly after bag-shelters had been formed (i.e. before significant herbivory occurred) and two mesh enclosures were placed on individual branches, one enclosure containing a bag-shelter with caterpillars and one control without caterpillars (to provide a measure of herbivory by other insects). Each enclosure contained a similar number of leaves. After one week the branches with enclosures were taken back to the laboratory for analysis. Every leaf in each enclosure was examined and the amount of damage was recorded. This procedure was carried out in May and June 1987 and February and March 1988. At the same time, bags were collected from adjacent trees and the number of caterpillars per bag determined. Combining these data provided an estimate of the total amount of damage in a caterpillar season. In order to relate this to the entire tree, leaves were counted on 25 percent of the canopy of 13 individual trees (which did not contain bag-shelters) of various sizes and multiplied by four to obtain total leaves per tree.

Further information on the effect of herbivory on the productivity of *A. acuminata* was obtained by tagging shoots of one year's growth of several trees within the study area. Ten trees were selected within Durokoppin Nature Reserve and ten along a narrow road verge. Five of the trees in each area contained bag-shelter caterpillars, the other five were kept free from caterpillars by removing

bag-shelters and painting Tanglefoot insect repellent gel around the trunks. Five shoots, all at about 3 m height and on the west side of the tree, were tagged on each selected tree. Recordings on each shoot were made at monthly intervals, commencing February 1987, of leaf gain or leaf loss and damage on the shoot.

In order to relate herbivory to the nutrient status of the tree, five samples of soil (top 5 cm), young (new season's) leaves and mature leaves of *A. acuminata* (each sample coming from one tree) were collected from a 50 x 50 m area within Durokoppin Nature Reserve and also from a 100 m stretch of one narrow road verge study site. These samples were dried and analysed for total N, P and K content, using the Kjeldahl digestion method, colorimetry and flame photometry respectively. The data were analysed using t-tests.

## Results

In April 1987 there was an estimated total of 10,940 *A. acuminata* trees on verges within the area (Table 1). The number of trees sampled in the 1988 survey was slightly different to the previous year, since 100 m transects were not examined in exactly the same locations. One-way analysis of variance indicated that there was a significant effect of verge width on the number of trees per km in 1987 ( $F_{2,212}=4.58$ ,  $p=0.011$ ) and 1988 ( $F_{2,233}=9.96$ ,  $p<0.001$ ). Comparison of means by the least significant difference (LSD) method indicated that this was due mostly to a greater number of trees in wide verges than in narrow verges in 1987 ( $p<0.001$ ) and 1988 ( $p<0.01$ ). Narrow and medium verges did not differ significantly in tree numbers per km in either year.

The estimated total number of bag-shelters of *O. lunifer* along verges in the area was 15,330 in the 1987 survey but less than 10% of this number in 1988 (Table 1). There was no effect of verge width on number of bag-shelters per km in 1987 ( $F_{2,213}=1.32$ , NS) or 1988 ( $F_{2,232}=0.76$ , NS). However, verge width did affect the number of bag-shelters per tree in both 1987 ( $F_{2,88}=5.03$ ,  $p=0.009$ ) and 1988 ( $F_{2,80}=3.28$ ,  $p=0.043$ ). This was due to a greater number of bag-shelters

Table 1

Numbers of trees of *Acacia acuminata* and bag-shelters of *Ochrogaster lunifer* along road verges in the study area, estimated from 100 m sections of different types of road verge during April 1987 and 1988 (one sample section per km of road verge type). Tree numbers differ between years because of differences in sections sampled (Mean ± SE).

	Width of Road Verge		
	Wide >20m	Medium ≈10m	Narrow <5m
Length of road system (km)	12.8	34.8	190
No. trees per km 1987	155±33	83±45	32±5
No. trees per km 1988	165±33	96±52	31±5
No. bag-shelters per km 1987	62.5±29.8	31.3±15.2	70.7±12.4
No. bag-shelters per km 1988	4.7±3.1	3.2±1.7	5.2±1.1
No. bag-shelters per tree 1987	0.4±0.3	0.4±0.2	2.2±0.3
No. bag-shelters per tree 1988	0.03±0.02	0.03±0.02	0.16±0.01

per tree on narrow verges than on either medium or wide verges in both years ( $p < 0.05$  in all comparisons by LSD). Medium and wide verges did not differ significantly in number of bag-shelters per tree in either year.

There were no bag-shelters in trees  $< 2$  m tall on road verges or in the reserve (Table 2). Of the other two possible height comparisons, there were significantly more bags per tree on road verges in the 2-3.9 m height class ( $F_{1,99} = 11.35$ ,  $p < 0.01$ ), and no significant difference between road verges and reserve in the 4-5.9 m height class.

Over all 6 plots in the reserve and on verges, mean number of bags per tree was significantly correlated with tree height ( $r = 0.648$ ,  $p < 0.05$ ,  $n = 48$ ) and crown diameter ( $r = 0.632$ ,  $p < 0.05$ ,  $n = 48$ ). Most bag-shelters were located near the top of large, tall trees or near the outside of the canopy, where new foliage is more abundant than elsewhere in the tree.

In the foliage consumption experiment, no differences were found in consumption between branches with and without bags on trees in the reserve at the start of the

experiment, and bags failed to develop. Results are thus given only for road verge trees. It was not possible to standardise the number of leaves per enclosure, but the mean number of leaves per enclosure varied only slightly between the four sampling periods (Table 3), and the differences were not significant. From the damage on each leaf, the total amount of damage per enclosure could be calculated in terms of number of leaf-equivalents consumed per enclosure. The mean number of leaf-equivalents consumed per bag-shelter was calculated by subtracting the value obtained for the controls from that obtained for the enclosures with caterpillars. Consumption was highest in February 1988 (mean = 65 leaf-equivalents). From this information, and the mean number of caterpillars per bag, the amount of foliage consumed per caterpillar per day was calculated, and the total amount of leaves consumed per bag per month was estimated. Again most foliage was consumed in February 1988 (mean = 259 leaf-equivalents) and least in June 1987 (mean = 142 leaf-equivalents). The data provide an estimate of the total amount of damage per bag-shelter during a caterpillar season as being equivalent

Table 2

Tree height, crown diameter and number of bag-shelter colonies of *Ochrogaster lunifer* on trees of *Acacia acuminata* of different height classes within the nature reserve and on a roadside (mean  $\pm$  SE).

Reserve	Height Class (m)				
	0-1.9	2-3.9	4-5.9	6-7.9	>8
Mean tree height (m)	1.48 $\pm$ 0.27	3.08 $\pm$ 0.49	5.02 $\pm$ 0.77	NA <sup>1</sup>	NA
Mean crown diameter (m)	0.57 $\pm$ 0.21	1.23 $\pm$ 0.14	2.69 $\pm$ 0.66	NA	NA
Mean number of bags per tree	0.00	0.20 $\pm$ 0.45	3.60 $\pm$ 1.93	NA	NA
Roadside	Height Class (m)				
	0-1.9	2-3.9	4-5.9	6-7.9	>8
Mean tree height (m)	1.42 $\pm$ 0.39	3.24 $\pm$ 0.24	5.24 $\pm$ 0.30	6.72 $\pm$ 0.43	9.10 $\pm$ 0.66
Mean crown diameter (m)	0.64 $\pm$ 0.34	1.74 $\pm$ 0.62	4.21 $\pm$ 0.91	5.93 $\pm$ 1.13	5.34 $\pm$ 0.47
Mean number of bags per tree	0.00	0.40 $\pm$ 0.54	2.60 $\pm$ 1.82	3.60 $\pm$ 2.07	11.60 $\pm$ 3.58

<sup>1</sup>NA = not available

Table 3

Leaf consumption by *Ochrogaster lunifer* in enclosures placed on branches of *Acacia acuminata* on road verges for one week each month during the 1987 and 1988 caterpillar season. All values are mean  $\pm$  SE ( $n = 8$ ). Italic figures represent estimates of leaves consumed per bag-shelter per month and of total consumption per colony over one season.

Month	Year	Numbers of leaves:					Estimated no. leaves consumed per bag-shelter per month	
		Total leaves in enclosure	Consumed in enclosure with caterpillars	Consumed in enclosure without caterpillars	Estimate of no. consumed by caterpillars in one week	No. of caterpillars per bag ( $n = 5$ )		Estimated foliage consumed per caterpillar per day (g wet wt)
January							129	
February	1988	174 $\pm$ 36	73 $\pm$ 24	8 $\pm$ 4	65	63 $\pm$ 5	0.028	259
March	1988	161 $\pm$ 27	64 $\pm$ 21	8 $\pm$ 4	56	59 $\pm$ 8	0.026	247
April								222
May	1987	188 $\pm$ 42	54 $\pm$ 18	9 $\pm$ 5	45	22 $\pm$ 3	0.055	198
June	1987	146 $\pm$ 34	43 $\pm$ 16	10 $\pm$ 5	33	15 $\pm$ 3	0.061	142
Total estimated consumption (leaves per bag-shelter per season)							1197	

to approximately 1200 leaves. This is equivalent to the total amount of foliage on a tree almost 2 m tall (Fig 1). It is recognized that this estimate is affected by the techniques employed, and that caterpillars in an enclosure may exhibit different feeding behaviour to caterpillars in a normal tree.

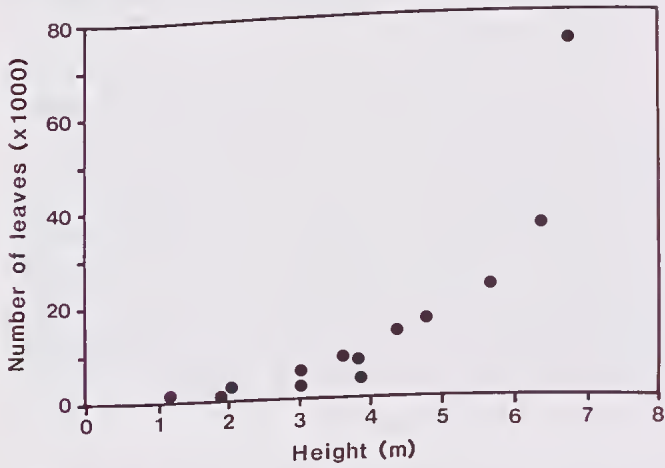


Figure 1. Relationship between height of *Acacia acuminata* trees and number of leaves present. Maximum tree height encountered was <7m.

Shoots on the *A. acuminata* trees on the road verge were longer and supported more leaves than those on trees from the reserve (Table 4). There was generally very little leaf loss on trees from the nature reserve (Fig 2), and there was no significant difference in leaf loss or gain on trees with and without caterpillars. Numbers of leaves per shoot were significantly higher on trees along the verge. The caterpillar-free trees on the road verge followed the same trend as those in the reserve, with very little leaf loss during the experiment. There were, however, highly significant differences in April-July between trees without and trees with caterpillars on the verge (Table 4). An average of 6.9 leaves per shoot were lost and 9.3 leaves per shoot were gained on trees with caterpillars (Fig 2). Here, new growth took place in July, at least two months earlier than on the trees in the reserve and on the caterpillar-free trees of the road verge. Several shoots were completely stripped of leaves, while others lost very few. This depended on their location on the tree; most damage usually occurred on the branch on which the bag-shelter was located.

Levels of N, P and K were higher in young (new season's) leaves than in mature ones in both the road verge and reserve (Table 5). Mature leaves collected from the road verge contained significantly more N and P than those from the nature reserve. No significant difference was detected in levels of K in mature leaves from both areas, and there were no significant differences between

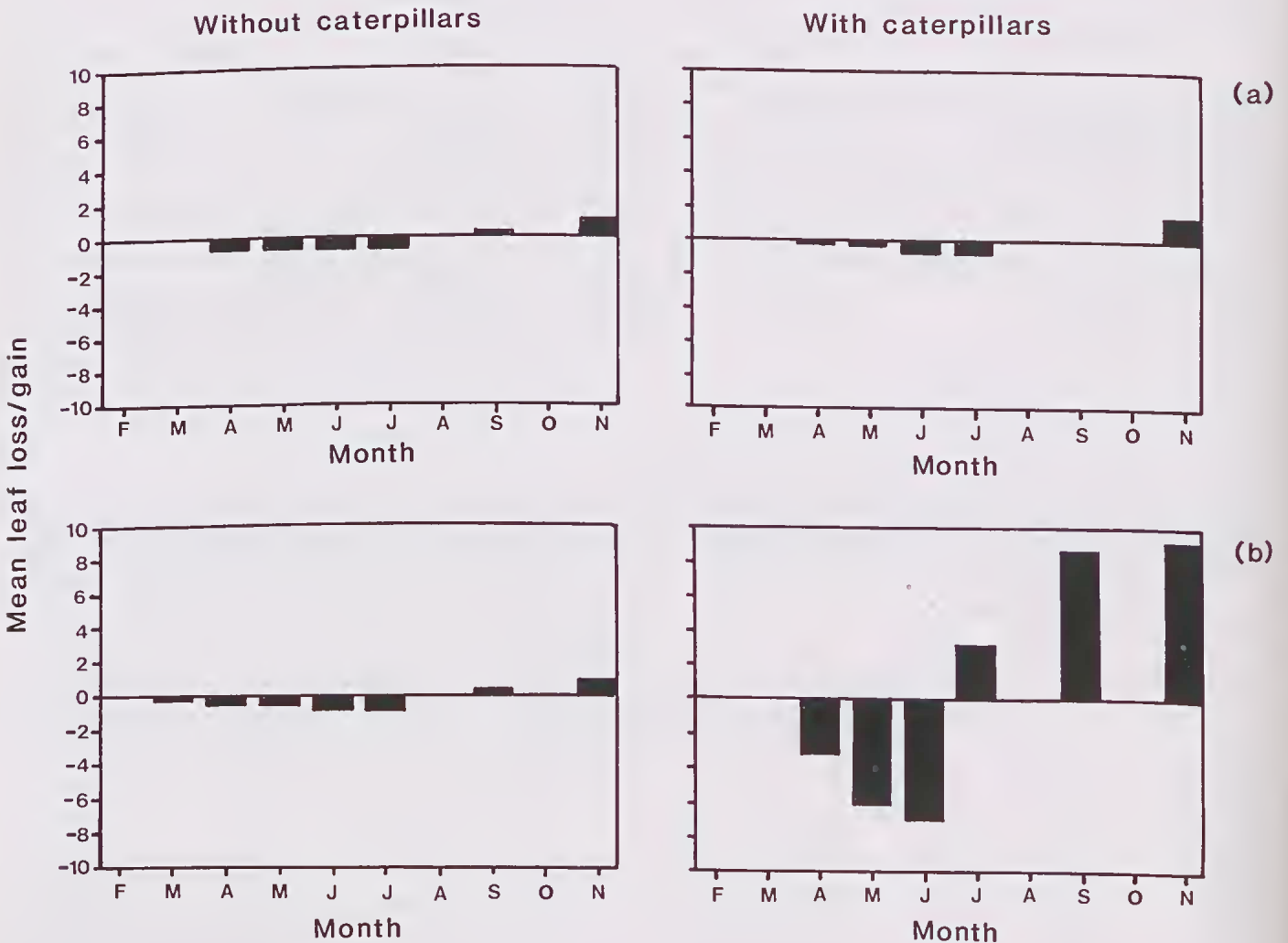


Figure 2. Leaf loss and leaf gain on tagged shoots on *Acacia acuminata* trees with and without the presence of caterpillars in (a) Durokoppin Nature Reserve, and (b) a narrow road verge. No data are available for August and October (n=5).

nutrient levels in young leaves collected from the road verge and those from the nature reserve. Soil samples from road verges contained significantly more N than those taken from within the reserve.

### Discussion

The fragmented landscape of the Western Australian wheatbelt has undergone many biotic and environmental changes due to the rapid clearing for agriculture over the last century, and these changes are continuing (Saunders 1989). It is to be expected that large remnant areas will be less affected by these changes than smaller ones (Saunders *et al.* 1991), and it seems likely that smaller areas, and in particular, the long thin strips constituting roadside corridors may be unable to persist in the face of these changes. It is thus important to assess the likely threats to these corridors and determine whether management effort should be put into ameliorating these threats. Our study

illustrates one such threat posed by periodic outbreaks of the moth *O. lunifer* and the resulting defoliation of road verge trees, especially on narrow verges.

The distribution of *O. lunifer* populations in the study area was very patchy in both years studied. No bag-shelters developed fully within the nature reserve, despite the presence of small bags on several trees earlier in the year. In both road verges and in the reserve, there was a preference for taller trees, perhaps because taller trees have more available canopy for moths to lay eggs. Alternatively, the taller trees may offer more foliage as a food source for caterpillars. Our data indicate that trees less than 2 m tall may not provide sufficient foliage for a colony to reach maturity.

In the reserve there was no significant difference in leaf loss and leaf gain between trees with or without caterpillars, since most colonies died out. Pronounced insect defoliation was, however, seen on trees with caterpillars on the road verges. Here, several shoots were defoliated,

Table 4

Mean numbers of leaves ( $\pm$ SE) on tagged shoots of *Acacia acuminata* on reserve and road verge sites in 1987, with and without caterpillars (n=5), and results of t-tests on comparisons between sites (ns=not significant, \* p<0.05, \*\*\* p<0.001). ND=no data available.

	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Without Caterpillars										
Verge	10.4 $\pm$ 0.3	10.2 $\pm$ 0.2	9.9 $\pm$ 0.3	9.9 $\pm$ 0.3	9.6 $\pm$ 0.4	9.6 $\pm$ 0.4	ND	10.0 $\pm$ 0.4	ND	10.6 $\pm$ 0.7
Reserve	7.3 $\pm$ 0.9	7.2 $\pm$ 1.0	6.5 $\pm$ 0.6	6.5 $\pm$ 0.6	6.4 $\pm$ 0.6	6.4 $\pm$ 0.6	ND	6.6 $\pm$ 0.6	ND	7.4 $\pm$ 0.7
With Caterpillars										
Verge	9.8 $\pm$ 0.3	9.8 $\pm$ 0.3	6.7 $\pm$ 0.4	3.8 $\pm$ 0.8	2.9 $\pm$ 0.8	6.1 $\pm$ 1.1	ND	11.7 $\pm$ 1.3	ND	12.2 $\pm$ 1.1
Reserve	7.1 $\pm$ 1.1	7.1 $\pm$ 1.1	6.9 $\pm$ 1.1	6.8 $\pm$ 1.2	6.4 $\pm$ 1.2	6.4 $\pm$ 1.2	ND	6.5 $\pm$ 1.2	ND	8.0 $\pm$ 0.8
Verge without vs verge with caterpillars	ns	ns	***	***	***	*	ND	ns	ND	ns
Reserve without vs reserve with caterpillars	ns	ns	ns	ns	ns	ns	ND	ns	ND	ns
Verge without vs reserve without caterpillars	*	*	*	*	*	*	ND	*	ND	*
Verge with vs reserve with caterpillars	*	*	ns	ns	*	ns	ND	***	ND	***

Table 5

Mean nutrient levels  $\pm$  SE (mg g<sup>-1</sup>) (n=5) in mature and young leaf and soil samples collected from reserve and verge areas with results of t-tests on comparisons between means (ns=not significant, \* p<0.05; \*\* p<0.01).

Site	Nutrient Level								
	N		P		K				
	Mature	Young	Mature	Young	Mature	Young			
Leaves:									
Road verge	35.49 $\pm$ 2.47	*	43.64 $\pm$ 1.49	0.53 $\pm$ 0.02	**	0.71 $\pm$ 0.02	3.46 $\pm$ 0.22	**	7.82 $\pm$ 0.57
Reserve	27.11 $\pm$ 0.44	**	41.65 $\pm$ 1.56	0.41 $\pm$ 0.03	**	0.64 $\pm$ 0.03	4.07 $\pm$ 0.84	**	8.13 $\pm$ 0.31
Soil:									
Road verge	0.40 $\pm$ 0.08	*		0.07 $\pm$ 0.01	ns		0.29 $\pm$ 0.03	ns	
Reserve	0.11 $\pm$ 0.05			0.07 $\pm$ 0.01			0.18 $\pm$ 0.03		

resulting in a greater overall leaf loss. However, soon after defoliation new shoots were formed on the trees. On defoliated trees, new shoots were formed in July, whereas on undefoliated trees, this did not happen until September. This resulted in the trees in the nature reserve putting on very little new growth, whereas trees in the verge that were defoliated supported a large amount of new growth, and very little old foliage.

High levels of nutrients, in particular nitrogen, as a result of fertilizer input or other factors have been associated with high insect populations (Port & Thompson 1980, Myers & Port 1981). Investigations have shown that increased nutrient levels, particularly nitrogen, may increase larval development and survival to the adult stage (Mattson 1980, Cates *et al.* 1987, Landsberg *et al.* 1990). Young leaves in both reserve and road verge sites contained significantly higher nutrient levels than mature leaves, but mature leaves on road verge trees had significantly greater levels of N and P than trees in the reserve. This was matched by higher levels of soil N on verges than in the reserve, although P values did not differ significantly between verges and the reserve. Elevated N on road verges could be due to sheep urine and faeces, given that sheep are periodically driven along the roads. Cale & Hobbs (1991), on the other hand, found significantly elevated levels of P on road verges compared with reserve areas. There is thus an indication that soil and foliar nutrient levels are higher in the road verges than in the reserve. The relationship between soil and foliar nutrient levels is not clear, however, especially since *A. acuminata* possesses root nodules containing *Rhizobium*, a nitrogen-fixing bacterium.

Higher foliar nutrient levels and increased proportions of young leaves may make road verge foliage more attractive to caterpillars, and lead to repeated attacks. Invertebrate herbivory has often been considered a major factor associated with the phenomenon known as 'rural dieback' or 'eucalypt dieback' in Australia (Landsberg *et al.* 1990). Self-perpetuating defoliation cycles have been hypothesised by Landsberg & Wylie (1983) and Landsberg (1990a) in eastern Australia, while Landsberg (1990b) also hypothesised that increased soil nutrient availability could initiate such cycles. Repeated defoliation could cause severe stress and result in the death of the trees especially if coupled with climate-induced stress (White 1969). Lamont & Southall (1982) have also found that mistletoes are more abundant on *A. acuminata* trees in road verges than in undisturbed vegetation. This may add a further source of stress to these trees. We noted tree mortality at several of our road verge sites, particularly in narrow verges.

A further factor which may influence insect abundances in road verges versus larger reserves is the relative number of predators. There is little information available on the predators of *O. lunifer* but there is evidence from other studies that fragmentation and habitat loss have affected the numbers and diversity of insectivorous birds in the area (Lynch & Saunders 1991). Although there is little evidence to suggest that abundance or diversity of insectivorous birds differ greatly between corridors and remnant areas (Cale 1990, Arnold & Weeldenburg 1990), there is a strong correlation between road verge width and abundance of bird species (Arnold & Weeldenburg 1990, Saunders & de Rebeira 1991). This is consistent with significantly greater incidence of bag moths on narrow verges.

Although we were not able to establish the causes of the observed patterns of *O. lunifer* herbivory, we have shown that trees on road verges, especially narrow verges, are more susceptible to attack than trees within intact vegetation in a large nature reserve. Since caterpillar colonies established but failed to survive within the reserves,

herbivore damage to trees was minimal compared with that found on road verges. The effects of the outbreaks of *O. lunifer* were thus restricted to road verge tree populations. This observation provides an indication that the dynamics of the road verge vegetation are significantly altered, as has been found in other studies in the area (Cale & Hobbs 1991).

The road verges appear to be much less buffered against disturbing agents, such as the defoliating insects studied here. This is predictable from a consideration of the increased edge effect and influence of the surrounding matrix in corridor vegetation (Saunders *et al.* 1991, Loney & Hobbs 1991, Soul & Gilpin 1991). Narrow verges, in particular, are at increased risk of losing trees through defoliation. These verges make up by far the greatest proportion of the corridor network in the study area, and this is generally true over much of the Western Australian wheatbelt. This has important implications for the long-term management of these corridors, and brings into question the long-term viability of existing corridor vegetation and of corridors currently being re-established. In order to retain a corridor network in the area, it may be necessary to manage the corridor vegetation more intensively than is necessary in the case of larger remnant areas.

Alternatively, the long-term viability of the narrower corridors may be enhanced by changing their design and structure through the establishment of broader verges, for instance by encouraging farmers to plant several rows of trees adjacent to road verges. This would not only reduce defoliation by *O. lunifer* but could also benefit the survival and dispersal of native species of conservation interest. In the long term, broader corridors are likely to be more viable in terms of the persistence of their resident populations, and potentially of greater value for species dispersal. Widening of existing narrow corridors is thus an important option to consider in the management of corridor networks. It seems that narrow corridors will not persist in the long term if their populations are reduced by herbivore-induced mortality. If they are considered important within the context of the overall conservation network, they need rapid attention before they disappear.

*Acknowledgements:* We thank L Atkins and S van Leeuwen for assistance in data collection and analyses, and Jill Landsberg and Janet Farr for constructive comments on earlier versions of the manuscript. Identification of insects was checked by the Australian National Insect Collection.

## References

- Arnold G W & Weeldenburg J R 1990 Factors determining the number and species of birds in road verges in the wheatbelt of Western Australia. *Biological Conservation* 53:295-315.
- Beard J S & Sprenger B S 1984 Geographical data from the vegetation survey of Western Australia. *Vegetation Survey of WA, Occasional Paper 2*. Vegmap Publications, Perth.
- Cale P 1990 The value of road reserves to the avifauna of the central wheatbelt of Western Australia. *Proceedings of the Ecological Society of Australia* 16:359-367.
- Cale P & Hobbs R J 1991 Condition of roadside vegetation in relation to nutrient status. In: *Nature Conservation 2: the Role of Corridors* (ed D A Saunders & R J Hobbs) Surrey Beatty and Sons, Chipping Norton, 353-362.
- Cates R G, Henderson C B & Redak R A 1987 Responses of the Western Spruce Budworm to varying levels of nitrogen and terpenes. *Oecologia* (Berlin) 73:312-316.
- Harris L D & Scheck J 1991 From implications to applications: the dispersal corridor principle applied to conservation of biological diversity. In: *Nature Conservation 2: the Role of Corridors* (ed D A Saunders & R J Hobbs) Surrey Beatty and Sons, Chipping Norton, 189-220.
- Hobbs R J, Wallace J F & Campbell N A 1989 Classification of vegetation in the Western Australian wheatbelt using Landsat MSS data. *Vegetatio* 80:91-105.

- Lamont B B & Southall K J 1982 Biology of the mistletoe *Anyema preissii* on road verges and undisturbed vegetation. *Search* 13:87-88.
- Landsberg J 1990a Dieback of rural eucalypts; response of foliar dietary quality and herbivory to defoliation. *Australian Journal of Ecology* 15:89-96.
- Landsberg J 1990b Dieback of rural eucalypts: the effect of stress on the nutritional quality of foliage. *Australian Journal of Ecology* 15:97-107.
- Landsberg J & Wylie F R 1983 Water stress, leaf nutrients and defoliation: a model of dieback of rural eucalypts. *Australian Journal of Ecology* 8:27-41.
- Landsberg J, Morse J & Khanna P 1990 Tree dieback and insect dynamics in remnants of native woodlands. *Proceedings of the Ecological Society of Australia* 16:149-165.
- Loney B & Hobbs R J 1991 Management of vegetation corridors: maintenance, rehabilitation and establishment. In: *Nature Conservation 2: the Role of Corridors* (ed D A Saunders & R J Hobbs) Surrey Beatty and Sons, Chipping Norton, 299-311.
- Lynch J F & Saunders D A 1991 Responses of bird species to habitat fragmentation in the wheatbelt of Western Australia: interiors, edges and corridors. In: *Nature Conservation 2: the Role of Corridors* (ed D A Saunders & R J Hobbs) Surrey Beatty and Sons, Chipping Norton, 143-158.
- Mattson W J Jr 1980 Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* 11:119-161.
- McFarland N 1979 Annotated list of larval food plant records for 280 species of Australian moths. *Journal of the Lepidopteran Society* 33 (supp.):1-72.
- Mills M B 1951 Bag-shelter caterpillars and their habits; pt. 1. *Western Australian Naturalist* 3:61-67.
- Mills M B 1952 Bag-shelter caterpillars and their habits; pt. 2. *Western Australian Naturalist* 3:84-92.
- Myers B G & Port B J 1981 Plant nitrogen and fluctuations of insect populations: a test with cinnabar moth-tansy ragwort system. *Oecologia* (Berlin) 48:151-156.
- New T R 1984 *A Biology of Acacias*. Oxford University Press, Melbourne.
- Noss R F 1987 Corridors in real landscapes: a reply to Simberloff and Cox. *Conservation Biology* 1:159-164.
- Panetta F D & Hopkins A J M 1991 Weeds in corridors: invasion and management. In: *Nature Conservation 2: the Role of Corridors* (ed D A Saunders & R J Hobbs) Surrey Beatty and Sons, Chipping Norton, 341-351.
- Port G R & Thompson J R 1980 Outbreaks of insect herbivores on plants along motor ways in the United Kingdom. *Journal of Applied Ecology* 17:649-656.
- Saunders D A 1989 Changes in the avifauna of a region, district and remnant as a result of fragmentation of native vegetation: the wheatbelt of Western Australia. A case study. *Biological Conservation* 5:99-135.
- Saunders D A & de Rebeira C P 1991 Values of corridors to avian populations in a fragmented landscape. In: *Nature Conservation 2: the Role of Corridors* (ed D A Saunders & R J Hobbs) Surrey Beatty and Sons, Chipping Norton, 221-240.
- Saunders D A & Hobbs R J 1991 The role of corridors in nature conservation: what do we know and where do we go? In: *Nature Conservation 2: the Role of Corridors* (ed D A Saunders & R J Hobbs) Surrey Beatty and Sons, Chipping Norton, 421-427.
- Saunders D A, Hobbs R J & Margules C R 1991 Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5:18-32.
- Saunders D A, Arnold G W, Burbidge A A & Hopkins A J M 1987 The role of remnants of native vegetation in nature conservation: future directions. In: *Nature Conservation: the Role of Remnants of Native Vegetation* (ed D A Saunders, G W Arnold, A A Burbidge & A J M Hopkins) Surrey Beatty and Sons, Chipping Norton, 387-392.
- Simberloff D & Cox J 1987 Consequences and costs of conservation corridors. *Conservation Biology* 1:63-71.
- Soul M E & Gilpin M E 1991 The theory of wildlife corridor capability. In: *Nature Conservation 2: the Role of Corridors* (ed D A Saunders & R J Hobbs) Surrey Beatty and Sons, Chipping Norton, 3-8.
- Turner A J 1921 An entomologist in the interior: pt. 2. *Queensland Naturalist* 1921:40-47.
- van Schagen, J J, Majer, J D & Hobbs, R J 1992 Biology of *Ochrogaster lunifer* Herrich-Schaeffer (Lepidoptera: Thaumetopoeidae), a defoliator of *Acacia acuminata* Benthham in the Western Australian wheatbelt. *Australian Entomological Magazine* 19:19-24.
- White T C R 1969 An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. *Ecology* 50:905-909.